

2020-10

Sorghum chemistry delineates levels of its susceptibility to weevils (*sitophilus* spp) and breeding strategies towards variety development; a review

Mwenda, Emmanuel T.

The Journal of Animal & Plant Sciences

<https://dspace.nm-aist.ac.tz/handle/20.500.12479/1246>

Provided with love from The Nelson Mandela African Institution of Science and Technology

REVIEW PAPER

SORGHUM CHEMISTRY DELINEATES LEVELS OF ITS SUSCEPTIBILITY TO WEEVILS (*SITOPHILUS* SPP) AND BREEDING STRATEGIES TOWARDS VARIETY DEVELOPMENT; A REVIEW

E. T. Mwenda^{*1,2}, J. H. Ringo² and E. R. Mbega¹

¹Department of Sustainable Agriculture and Biodiversity Ecosystem Management, School of Life Sciences and Bioengineering, The Nelson Mandela African Institution of Science and Technology (NM –AIST), P.O. Box 447 Arusha, Tanzania.

²Sorghum and Millets Research Program, Tanzania Agricultural Research Institute (TARI – Ilonga), P.O. Box 33 Kilosa, Morogoro, Tanzania.

Corresponding author's e-mail: mwenda@nm-aist.ac.tz, emmamwenda@yahoo.com

ABSTRACT

Weevils (*Sitophilus* spp) are serious pests that can damage sorghum grains in stores if not controlled. The infestation of sorghum by the pest can cause huge economic loss ranging from 15% to 75% depending on levels of susceptibility. While the weevil uses several infection mechanisms such as avoidance, adaptation and sequestration to arrest its host, the host plant has developed certain chemical mechanisms for defence. The weevil must overcome the hosts' defensive layers of chemical compounds such as protein resistant molecules, tannin, phenolics and flavonoids that confer antixenosis and or antibiosis functions in sorghum. Besides, the biochemical molecules present in sorghum are also responsible for modulating grain hardness and strength, which are important phenotypic parameters for grain resistance to weevil in sorghum. This paper reviews traits and or their associated produced chemical compounds in sorghum and reveals the gaps or need for incorporating appropriate desirable traits in sorghum through plant breeding techniques as a strategy towards management of grain weevils in sorghums.

Key words: Breeding, chemistry, genotypes, weevil - sorghum interaction.

INTRODUCTION

Sorghum (*Sorghum bicolor* L.) is a cereal crop largely used for food and forage, hay or silage and production of local brewers in semi-arid and arid tropics worldwide (Reddy *et al.*, 2008; Mukarumbwa and Mushunje, 2010; Macauley, 2015; Mafuru *et al.*, 2016). Its stem can be used for building, weaving, fencing, firewood and broom making (Ogolla *et al.*, 2016). Industrially, it can be used for production of fiber, starch, dextrose syrup, biofuels and alcohol (Sinha and Kumaravadivel, 2016). Worldwide, Sorghum ranks fifth among cereals with annual production of about 55.1 MT (Weledesemayat *et al.*, 2016; Oyier *et al.*, 2016). Despite its importance, there exist several production challenges such as decreasing soil fertility, use of unimproved genotypes, extreme drought insect pests and diseases. Of the pest, grain weevil (*Sitophilus spp.*) has been cited to be one of major biotic challenge of sorghum production especially in developing countries where proper management options are limited (Mofokeng *et al.*, 2016). The weevils cause damage by feeding and laying some eggs on grains when the crop is in the field and or during storage time, thus, reducing quality and quantity of the sorghum grains (Mendesil *et al.*, 2007; Ladang *et al.*, 2008). There are three major economic important

grain weevils species namely rice weevil (*Sitophilus oryzae*), granary weevil (*Sitophilus granarius*) and maize weevil (*Sitophilus zeamais*) (Young, 1977; CTA, 1998; Dal Bello *et al.*, 2000; Mofokeng, 2016). Grain damage by these weevil species is dependent on whether the sorghum genotypes are susceptible. In susceptible host, the weevil can succeed to attack the host where as in resistant sorghum genotypes, grain weevil attack is restricted (Huang *et al.*, 2013). War *et al.* (2012) associated three important aspects that make sorghum to be either susceptible or resistance to attack; the factors are genetic, morphological and biochemical composition of sorghum grain. These factors are the ones involved in plant defence mechanism against pests (Russell, 1966; Williams, 1978; Chandrashekar and Mazhar, 1999; Jadhav, 2006; Chandrashekar and Satyanarayana, 2006; Fürstenberg-hägg *et al.*, 2013). The crop contains starch, protein resistance molecules and secondary metabolites also known as phytochemicals including phenolic compounds including phenolic acids, coumarins, flavonoids and condensed tannin or proanthocyanidins; phytosterols and policosanols (Awika and Rooney, 2004; Dykes *et al.*, 2005; Saxena *et al.*, 2013; Vieira *et al.*, 2015). The secondary metabolites have been described to have deterrence, anti-feedant and toxicity properties that act as precursors to physical defence against insect pests

and pathogens (Bennett, 1994; Muzemu *et al.*, 2013) as shown in Figure 2.

The recommended weevil's control strategies in sorghum include provision of physical barriers, cultural methods such as sanitation; the use synthetic chemical insecticides, biological methods and the use of resistant cultivars (Mofokeng, 2016). Despite of its dominance the use of synthetic chemicals in sorghum storage have been implicated with high purchase costs to farmers, potential health effects from residuals and environmental pollution (Talebi *et al.*, 2011). Thus, causes fear among users of sorghum grains (Gracen and Guthrie, 2008). Sorghum resistance remains the best and sustainable strategy in controlling weevils (Chandrashekar and Satyanarayana, 2006). Biochemical molecules in sorghum grain are regarded as constitutive host plant resistance (War *et al.*, 2012). According to Bergvinson and Garcia-Lara, (2004); Gerrano *et al.* (2014); Abraha *et al.* (2015); Turner *et al.* (2016) these bio-chemical molecules are genetically controlled. Unfortunately, this information is not fully

deployed in developing resistant sorghum varieties to grain weevils particularly in developing countries where weevil infestation is much bigger. Understanding of chemistry in sorghum and its interaction with weevils would contribute to identification of reliable sources of weevil resistance to be utilised as parental materials in sorghum breeding. Resistant chemical molecules, breeding strategies and approaches have been explored in this paper.

Effect of grain weevil's infestation on sorghum: Figure 1 shows the effect of grain weevils infestation on sorghum; where kernel damage caused by weevil infestation reduces sorghum grain quality through weight loss, nutritional loss, growth of microbes (Mason and McDonough, 2012), decrease in the thiamine/protein content (Venkatrao *et al.*, 1958), accumulation of urine which increases chances of grain rancidity, poor seed germination and reduced market value of the crop (Mofokeng, 2016).

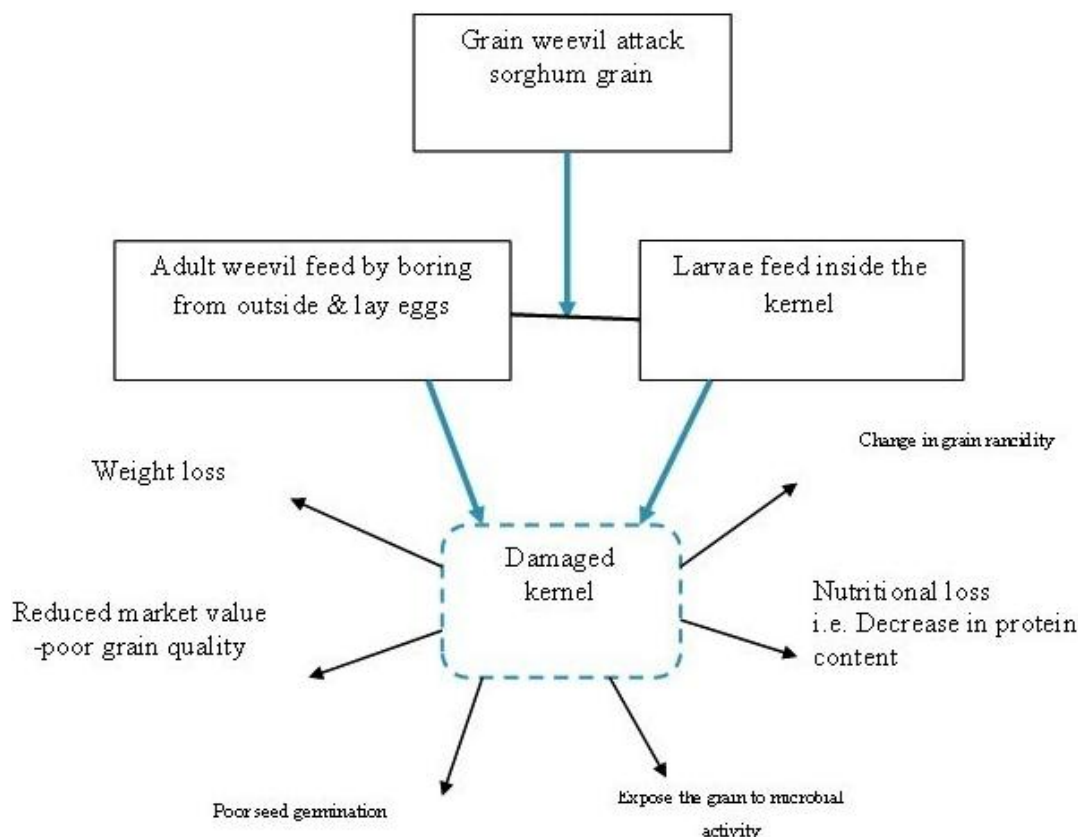


Figure 1. Effect of grain weevil's infestation on sorghum

Grain weevil attack strategies: Like any other insect pest, grain weevils use several strategies to attack sorghum grain including boring the kernel by adults, laying eggs in cavity and larvae feeding inside the kernel (Mason and McDonough, 2012). To ensure their survival, feeding and reproduction, grain weevils use several

strategies to overcome the grain or seed defence barriers; these include detoxification of toxic chemical compounds, avoidance mechanisms, sequestration of poison and alteration of gene expression pattern (Mello and Silva-filho, 2002).

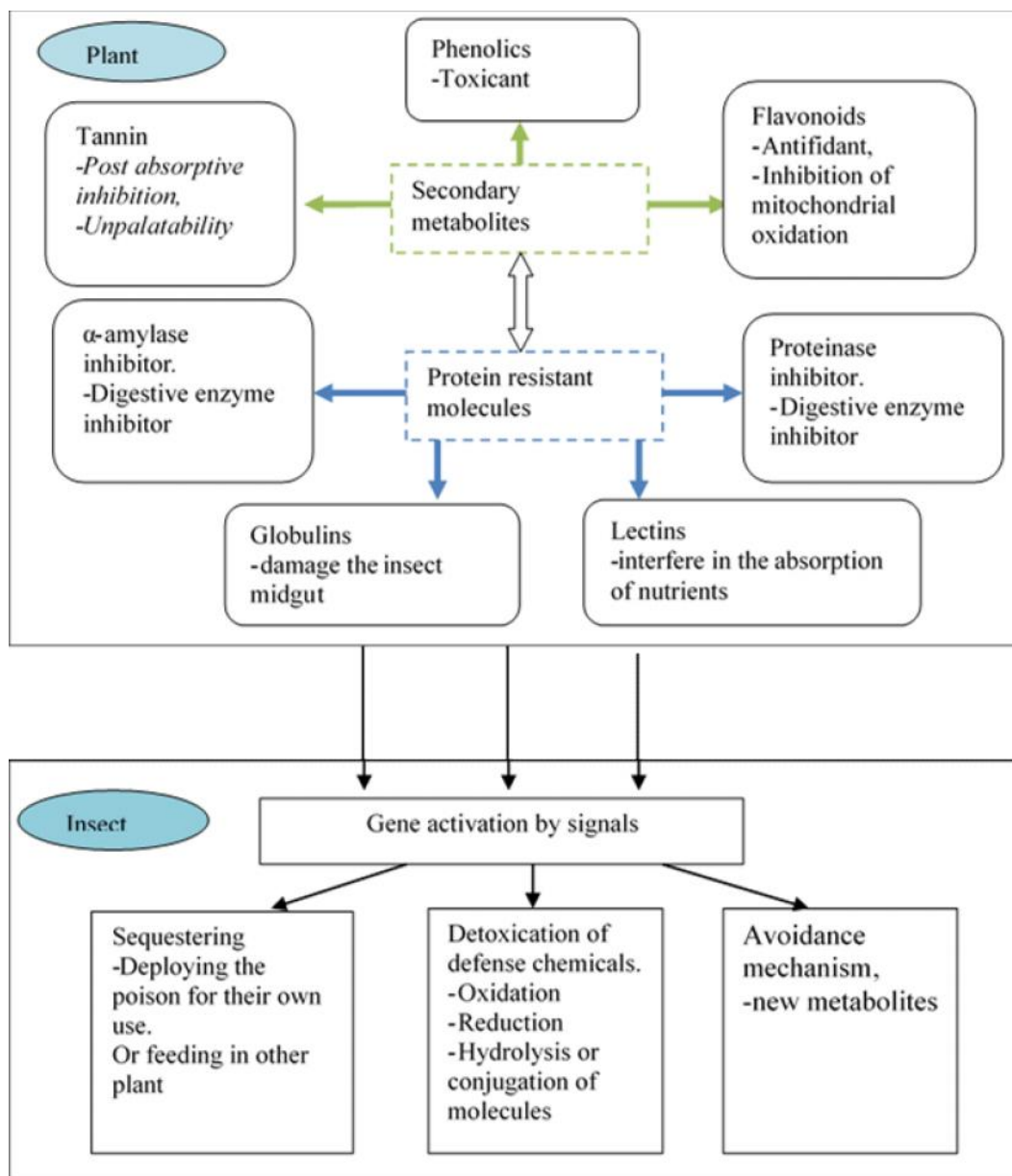


Figure 2. Plant – insect (grain weevil) interaction

Sorghum defence strategies against grain weevils: The complex interaction between sorghum and weevils comprises a diverse range of defence through sorghum grain resistance traits including antibiosis (resistance), antixenosis (deterrence) or non-preference and tolerance (Boots *et al.*, 2009; Kant *et al.*, 2015). These resistance traits control the level of damage from insect attack and when the interaction is in favour of the host sorghum grain, the weevil abundance can be altered (Painter, 1951; Huang *et al.*, 2013; Bustos-Segura *et al.*, 2014). Antixenosis and antibiosis defensive strategy makes use of biochemical compounds in sorghum grain; these chemicals can be described as constitutive host plant defences because chemical traits are formed prior to

insects attack (Huang *et al.*, 2013). However, it is possible to induce the response through genetic engineering to make defensive compounds constitutively produced in plants and provide potential means of developing resistant sorghum cultivars to insect (War *et al.*, 2012). In order for breeder to understand the antibiosis and antixenosis in sorghum genotypes a choice or no-choice laboratory procedures must be used (Dent, 2000).

Antibiosis resistance: Antibiosis resistance has an impact on grain weevils biology especially in the survival or longevity, development and oviposition or reproduction behaviour of the insect (Gu *et al.*, 2008).

According to Kant *et al.*, (2015) antibiosis resistance traits can harm or kill insect or slow its development and oviposition. Sharma (1993), have associated this type of resistance with higher concentration of tannin and protein. The higher the tannin and protein the higher the resistance in sorghum genotype. The antibiosis resistance may also be due to both biophysical and biochemical factors including presence of toxic materials such as secondary metabolites, absence of sufficient amount of nutrients and even nutrient imbalance (Mendesil, 2014). Secondary metabolites, for example, can repel or intoxicate insects while the defence protein can obstruct with insect digestion (Fürstenberg-hägg *et al.*, 2013). Therefore, antibiosis with other components of resistance seems to be potential strategy in breeding programs to develop resistant sorghum cultivars to insect pest such as grain weevil (Sharma, 1993).

Antixenosis: The term antixenosis has been originated from Greek word “xeno” which explains the ineffectiveness of a plant to be a host to anthropod (Smith, 2005). Antixenosis refers to non- preference of grain weevil in a resistant sorghum genotype as compared to a susceptible genotype; it, therefore, affects the insect (weevil) behaviour (Reddy *et al.*, 2002). During interaction of insect-plant, the insect tends to choose an alternative plant host. Non-preference explains the reason why some plants become less damaged than others as a response to insect pests. According to Kant *et al.* (2015) antixenosis or deterrence traits are always constitutively articulated and can be from grain colour, odour and even textures that discourage insect pest from feeding, absence of feeding stimuli injuring or killing an insect pest or just slowing its oviposition and development. Morphological/physical barriers on subject plants might cause insects to unrestraint efforts to oviposit and feed on non antixenous plant (Smith, 2005).

Resistant sorghum genotype could lack sufficient levels of secondary metabolites to stimulate insect oviposition, and feeding (Lattanzio *et al.*, 2006). Insect resistant plants possesses secondary metabolites that prevent herbivores from oviposition and feeding (War *et al.*, 2012); In addition, resistant sorghum genotype may possess chemicals that are toxic to insects after ingestion of plant materials (Huang *et al.*, 2013). Antixenosis is evident in cultivars of some crops such as sorghum with structures like glume and grain husk (Smith, 2005). Thus, Reddy *et al.* (2002) in the study on resistance to rice weevil in relation to antixenosis responses suggested the need for identification of greater levels of antixenosis to *Sitophilus oryzae* especially in developing parental lines when developing hybrids.

Tolerance: Tolerance refers to the ability of sorghum genotype to tolerate injury or recover from damage caused by insect abundance through compensatory physiological course (Koch *et al.*, 2016). It also refers to

plant response to insect, it differs with antibiosis and antixenosis on how it affects insect plant relationship, because antibiosis and antixenosis involves insect response to resistant plant host on oviposition, shelter and food (Gu *et al.*, 2008). According to Kant *et al.* (2015) tolerance traits do not negatively interact with insect pest but compensate for damage. However, there are still little available information on tolerance mechanism against insect pest (Koch *et al.*, 2016), thus understanding of applicability of tolerance mechanism in sorghum grain resistance against weevils is essential.

Overview of the nutritional components in sorghum grain: Nutritional chemical composition in sorghum grains has been widely reviewed (Khalil *et al.*, 1984; Kulamarva *et al.*, 2012; Mabelebele *et al.*, 2015). Sorghum is a source of nutrition molecules such as carbohydrate, protein, vitamins and minerals such as phosphorus (P), potassium (K), magnesium (Mg), iron (Fe) and zinc (Zn) (Virupaksha and Sastry, 1968; Clark *et al.*, 1990; Pontieri *et al.*, 2014; Ajiboye *et al.*, 2014; Badigannavar *et al.*, 2016). According to Prasad *et al.*, (2015) sorghum grain nutrients may determine food suitability to storage insect pests. For instance, Keskin and Ozkaya, (2013) found higher content of minerals in the wheat and flour samples infested by *Sitophilus granarius*, while the level of thiamine and riboflavin were found to be lower. However, there is an insufficient literature on the role of mineral elements in the weevil-sorghum interaction; therefore, more studies are needed to investigate the role of mineral elements in this antagonistic interaction. An understanding of the role of mineral elements in the interaction would help define the significance of these minerals in sorghum and enable to maximise the benefits from such minerals.

Starch in sorghum grain: Starch is a major chemical component of sorghum grain (Sang *et al.*, 2008), making up 69.5 - 83% of the endosperm (Wall and Blessin, 1969; Waniska *et al.*, 2004; Felix *et al.*, 2015). The starch granules of sorghum look like those of corn in size, range and shape, and their molecular structure shows linear chains of glucose linked by α -1,4 and α -1,6 glycosidic bonds forming two types of molecules namely amylopectin and amylose (Hernandez, 2012). About 70 – 80% of starch in sorghums is made up by amylopectin; with exception of waxy sorghums. The remaining 20-30% of starch in sorghum consist of amylose content. The proportions of amylopectin, amylase and glucan chains govern the structure of starch in sorghum (Mutisya, 2004).

There is a positive correlation between starch depth, arrangement and the extent of resistance to damage by the *Sitophilus* (Pendleton *et al.*, 2011). The higher the proportions of amylose the harder the grain, a trait that is controlled by a master gene which controls management of different biochemical events

(Chandrashekar and Mazhar, 1999). Chippendale (1972) and Longstaff (1981) reported the effect of dietary carbohydrates in cereals and its role in feeding behaviour, consumption, and survival of *S. oryzae* and found that weevils survived well on diets with 72% (w/w) cereal starches and amylopectin, but not in diets having amylase, cellulose and mono/disaccharides; therefore they concluded that there were significant contribution of amylopectin chains of cereal starches which provide feeding stimulant and important nutrient to *S. oryzae*. This is to say, starch content and its chemistry seem to be an interesting parameter and can be used to describe susceptibility of sorghum genotypes to *Sitophilus* spp. However, more research studies are needed to find out if dietary starch containing amylase can be a source of resistance in sorghum grain, and assess its potential in sorghum improvement programs in developing countries to develop resistant sorghum cultivars to weevils.

Protein component in sorghum grain: Protein is the second major nutritional component in sorghum grain (Kulammarva *et al.*, 2012), and the content of protein varies between sorghum genotypes (Sastry *et al.*, 1986). The variation in grain composition may be due to climatic conditions, fertilizer application and soil types where sorghum is grown (Ebadi *et al.*, 2005). Protein content in sorghum genotypes ranges between 7.3 – 15.6% (Hulse *et al.*, 1980). In irrigation schemes, grain yield increases but protein content drops from 9.5% to 8.3% (Balko, 1975). Crop applied with nitrogen fertilizer sources boosted both protein and yield (Wall and Blessin, 1969; Salem, 2015). The total nitrogen N content on a dry basis of sorghum ranges from about 1-3% (Mosse *et al.*, 1988). Most of sorghum genotypes have deficient essential amino acids such as lysine, threonine, tryptophan and cysteine (Salunkhe *et al.*, 1977). Protein in sorghum is classified based on the solubility properties such as glutelin (44%), prolamin (26%), albumin and globulin (15%) (Ratnavathi and Patil, 2013). Prolamin subfamily include zeins and kafirin (Holding, 2014). Sorghum prolamins, termed kafirins, are categorized into subgroups a, b, and c (Kumar *et al.*, 2012). It appears that the biochemical basis has an implication on kernel hardness due to presence of prolamins (Holding, 2014), where the hard grains and vitreous part of the grain have c-prolamins which form the cement and a-prolamins forming bricks, the reason being that prolamins shapes the protein bodies through formation of disulphide bonds between proteins, thereby forming both physical and chemical (nutritional) barriers because of its resistance to digestion by grain weevil (Chandrashekar and Satyanarayana, 2006). The amount of prolamins in the endosperm and protein body and its distribution can be affected by the genetic and environmental conditions (Chandrashekar and Mazhar, 1999); for instance, sorghums grown under limited nitrogen are smaller in

size and lack vitreous endosperm, because of smaller and less abundance of zein protein bodies, which fails the formation of glassy like structure, because certain ration of protein bodies, starch and viscous cytoplasm are needed (Holding, 2014). Also the amount of resistance to grain damage can be determined by kernel texture such as hardness (vitreous) and soft endosperm (opaque) (Wu *et al.*, 2010; Holding, 2014). This information implies that sorghum genotypes with less vitreous endosperm are more susceptible to grain weevils.

According to Mello and Silva-filho (2002), in crops like legumes, plant defence is associated with an array of storage protein in seeds with entomotoxic properties including α -amylase, proteinase inhibitors, lectins and also globulins. These protein fractions can also be found in sorghum grain and is associated with grain resistance to *Sitophilus* spp. (Boisen, 1983; Nwosu *et al.*, 2015). During interaction these molecules interfere with nutrients absorption and or inhibit digestive enzymes of insect especially when lectin makes contact with glycoprotein (Mello and Silva-filho, 2002). The α -Amylase Inhibitors function as digestive enzyme inhibitor and can be found in many plants including sorghum grain and are directed to interact with α -amylases from insects used for starch breakdown, as a result restrain *Sitophilus* spp. during interaction (Fürstenberg-hägg *et al.*, 2013).

Various studies investigated the relationship between protein concentration and number of adult's weevil emergence and grain damage parameters. For instance, Murthy and Ahmed (1978) investigated eight sorghum varieties against storage weevil and results obtained indicated a positive correlation between number of adults emerged and protein content in different sorghum varieties; where genotype Y-75 had the lowest number of adults emergence and had lower protein content. Pradeep (2013) reported a positive correlation between sorghum protein content and the grain damage and population build-up of the *S. Oryzae*, where an increase of one milligram in protein content of the sorghum grain the grain damage increased by 0.85 per cent, and the population build-up of weevils increased to an extent of 0.50%. Nwosu *et al.* (2015) found that the susceptibility of maize to *Sitophilus zeamais* were increasing as protein level increases. However, Goftishu and Belete (2014) reported that the most important cause of resistance in sorghum against *Sitophilus zeamais* are lysine content in the grain, where the higher concentration of lysine in the genotype the higher resistant genotype it is. Thus, it is important to understand chemistry related to protein and associated resistant protein molecules in grain sorghum; due to its contribution in grain structure, grain strength and resistance to insect pest. Screening effort for reliable sources of protein and selection of appropriate breeding

strategy to transfer this trait into farmers preferred varieties are needed.

Review of secondary metabolites in sorghum grain:

Apart from nutritional chemical molecules, sorghum grain is rich in Phytochemicals, also known as secondary metabolites or anti-nutritional factors (Awika and Rooney, 2004). Phenolic compounds in sorghum have variety of genetically dependent levels including phenolic acids, condensed tannin and flavonoids (Dobie, 1977; Torres *et al.*, 1996; Dykes and Rooney, 2006; Dykes and Rooney, 2007). Phenolic compounds in sorghum grain can also be divided into tannin and non-tannin polyphenols, where the tannin sorghums have proanthocyanins as a component of their phenolic compounds but do not have tannic acid or hydrolyzable tannins (Chandrashekar and Satyanarayana, 2006).

These chemical compounds are the basis of antibiosis to storage pests such as grain weevil (Torres *et al.*, 1996; Kant *et al.*, 2015), and therefore, associated with weevil resistance, and thus, signifies its applicability in sorghum breeding for resistant cultivars (Sharma *et al.*, 2005). To breed varieties with high phenolic compounds it needs to screen many genotypes to get reliable sources. Dykes *et al.* (2014) pointed out various techniques used to determine relative phenolic levels among sorghum genotypes including; colorimetric methods such as Prussian blue, Folin-Ciocalteu, vanillin/HCl, butanol-HCl and ferric ammonium citrate, and; Other methods used to identify and quantify the specific phenolic compounds including High performance liquid chromatography (HPLC) attached with photodiode array (PDA), mass spectroscopy (MS) detectors and fluorescent. The role of phenolic compounds such as phenolic acid, condensed tannin and flavonoids in resistance against grain weevils is reviewed as under:

The role of phenolic acids in sorghum grain resistance against grain weevil:

The phenolic acids of sorghum are present as benzoic or cinnamic acid derivatives (Awika and Rooney, 2004). Phenolic acids and their derivatives are everywhere in the plant kingdom; this implies that all sorghums contain phenolic acids (Dykes and Rooney, 2006) in various forms including soluble and bound forms, and plays greater role in cell wall structure (by assembling phenolic compounds, structural proteins, polysaccharides, and other cell wall materials) and defence. Phenolic amines and the soluble phenolics were known to lower insect attacks in grain; for example, phenolic amines are known to prevent glutamate dependent neuron receptors in insects, the compound is contained in the aleurone (Bergvinson and Garcia-Lara, 2004).

The phenolic acids were reported to be in higher concentration in the pericarp and or cell walls of the endosperm, in addition the phenolic acid content in cereals were found to have an association with hardness

of the grain which can be related to the mechanical contributions of phenolic dimers to the grain cell wall strength, it is also interesting to know that aleurone layer has phenolic acid amines containing toxic effects to insects (Pradeep, 2013). Bergvinson and Garcia-Lara (2004) reported that the presence of peroxidases and protein inhibitors build grain resistance against insects by catalysing the polymerization of phenolic acids in pericarp which limit insect attack. The presence of phenolic acid in sorghum is also associated with pigmentation of the grain (Lattanzio *et al.*, 2006).

Various studies indicated a negative correlation between level of phenolic acid and sorghum grain damage and population build-up of the *S. oryzae*; for example, Pradeep (2013) concludes that an increase in phenol for one milligram, decreases sorghum grain damage and population build-up of weevil by 0.5%. Moreover, the study conducted to assess the function of phenolic acids on hardness of eight maize and sorghum cultivars, and revealed that the harder grains had higher concentration of phenolic acids than the soft grains; therefore, one can deduce that the content of phenolic acids is a useful indicator of grain hardness and is useful when discriminating hard and soft sorghum cultivars (Chiremba *et al.*, 2012). Considering the importance of phenolic acids in developing grain strength and antibiosis effect against weevils, a better understanding on the best mechanism to increase its levels in susceptible sorghum cultivars is critical to elevate sorghum resistance to weevils.

The role of tannin in sorghum grain resistance against grain weevil:

Tannin is referred to complex phenolic polymers with aliphatic and phenolic hydroxyl groups and or carboxyl groups (Hagerman, 2002). There is a great variation of tannin content between sorghum genotypes; For instance, sorghum cultivars having pigmented testa contain condensed tannins or proanthocyanidins (Waniska, 2000; Dykes and Rooney, 2006; Dykes *et al.*, 2014). Thus, there is a great relationship between grain colour of sorghum and the tannin content (Sedghi *et al.*, 2012). It is important to note that, the pericarp colour of sorghum is not the reliable indicator of presence of tannin (Rooney and Miller, 1981). The biosynthesis is controlled by Tan1 gene which code for WD40 protein control for tannin biosynthesis in sorghum (Wu *et al.*, 2012). Tannin possesses a strong feeding deterrent to weevil and, therefore, considered as a defensive phytochemical (Bennett, 1994; War *et al.*, 2012). Various literatures documented the relationship existing between condensed tannin and sorghum grains resistance to weevil attack (Ramputh *et al.*, 1999; Hernandez, 2012).

For example, brown sorghums with high tannin levels have higher resistance to insect attack (Wongo, 1998). Ramputh *et al.* (1999) report that the

soluble phenolic content consisting primarily of proanthocyanidins can be an indicator of resistance to *S. oryzae* in sorghum grain. Studies indicated the implication of tannin levels on weevils infestation; for instance, Pradeep (2013) reported a negative correlation first with grain damage and second with population build-up of the *S. oryzae*; where in every one milligram increase in tannin content of the sorghum grain had decreased the grain damage to the level of 0.90% and population build-up of *S. oryzae* to the level of 0.69%. More understanding on the significance of tannin levels on susceptibility of sorghum grain to insect pest is critical to breeders, including the methods of elevating its level in susceptible genotypes to prevent weevil's damage or developing sorghum cultivars with higher tannin content.

The role of Flavonoids in sorghum-weevil interaction:

Dykes *et al.* (2009) reported that sorghums with red and or purple plant colour had the highest concentration of 3-deoxyanthocyanins, and those with the black pericarp had the highest. Flavonoids plays a defensive task in plants by affecting the behaviour, growth and development of a number of insects (Lattanzio *et al.*, 2006). In sorghums, the main flavonoid derivatives are the flavans containing double bond between C3 and C4 and hydroxylated at C3 are anthocyanidins (Waniska, 2000), mainly flavanols, isoflavones, flavanones, flavones, and anthocyanins) (Dicko, 2005). Red pericarp sorghums with tan secondary plant colour were reported to have the highest levels of flavones, in addition Flavanones were also found in sorghum genotypes with a red pericarp; and secondary plant colour had no influence on the level of flavanones, these findings indicate that the level and composition of flavonoid were affected by sorghum genotype (Dykes *et al.*, 2009). Flavonoids are associated with grain defence against insect pests through toxicity and feeding deterrent (Lattanzio *et al.*, 2006). Therefore, this information may assist sorghum breeders to develop sorghum cultivars with required levels of flavonoids. There is a need to research more on the role of flavonoids in sorghum and concentration needed to bring deterrent effect to weevils. However, screening for genotypes with higher flavonoids concentration will provide breeders with reliable sources of this compound to be used in developing resistant cultivars to weevils.

Kernel phenotypic aspects conferring resistance to weevils: There is a correlation between chemical properties and kernel phenotypic aspects. In sorghum, phenotypic aspects are heritable traits that could assist sorghum breeders in selection of traits of interest for breeding purposes including resistance to insect pests. Heritable kernel physical traits include seed size, presence of testa, color, pericarp thickness and hardness or kernel strength (Geleta and Labuschagne, 2005; Prajapati *et al.*, 2018). According to Mofokeng *et al.* (2017) breeding for resistance to insects entails

knowledge on heritability of a particular trait. For this reason, there is a need of understanding sorghum kernel physical aspects convening resistance to weevils to come up with the best breeding strategies.

Kernel strength: Variation in textural aspect is a function of genetic and the environmental interaction. Kernel strength is attributed by the presence of prolamin and cell wall structure (Holding, 2014); harder sorghum kernel consists of higher concentration of kafirins (Chiremba, 2012). Kernel strength present useful resistance trait against insect pests. Hard grain seems to resist weevil attack than softer grain. For instance, Russell (1962) and Russell (1966) reported low oviposition rate, fewer eggs and short adult life in the harder sorghum grains. Bamaïyi *et al.* (2007) reported low susceptibility in genotypes ICSV1079BF, BES, ICSV247, ICSV111, and ICSH89009NG confirming the role of kernel strength in resistance against insect pest. Prasad *et al.* (2015) reported a positive significant relationship between 100 seed weight, median development period and hardness. Therefore, there is an urgent need of selecting suitable sources for kernel strength and identify the best breeding strategies to improve sorghum cultivars for sustainable management of weevil infestation in sorghum.

Pericarp color and thickness: According to USDA (2013) pericarp is an outer layer of sorghum kernel fused to seed coat. Pfeiffer and Rooney (2015) revealed that pericarp colour could be an indicator of certain biochemical in sorghum; for instance, black pericarp is correlated with higher levels of phenolic compounds. Pericarp color in sorghum is genetically controlled by R and Y genes (Earp *et al.*, 2004); while, Z gene control pericarp thickness. Dykes and Rooney (2006) revealed that homozygous recessive results into thick pericarp and the dominant gene result into thin pericarp. Earp and Rooney, (1982) exposed differences on genotypes based on pericarp thickness. The variation in pericarp thickness in sorghums is mainly due to difference in starch granules within the mesocarp; where thin pericarp are intensely bound to sorghum kernel (Earp *et al.*, 2004). Regarding the role of pericarp in insect resistance, undamaged pericarp convene more resistance than damaged pericarp. However, thicker pericarp are more susceptible to insect damage; further, grain coat features discourage oviposition due to kernel hardness and presence of enzymes (Williams, 1978; Dasbak *et al.*, 2009). Moreover, testa in sorghums is genetically controlled by B1 and B2 genes; testa thickness varies from 8 to 40µm (Earp and Rooney, 1982). Purple and brown colour testa is correlated with tannin content in sorghums (Cheng *et al.*, 2009). Therefore, presence of testa, color and pericarp thickness in sorghum provides important information for phenotypic selection when breeding weevil resistant sorghum cultivars.

Seed size: Kernel size play crucial role in grain resistance to weevil; larger kernel size have been associated with easiness to weevil attack, as large surface area supports oviposition and food availability for the larva. Russell (1962); Wongo (1990) and Stejskal and Kučerová (1996) pointed out that female weevil laid more eggs in larger kernels (>20 mg) mainly for larvae survival and large progeny size. Hence, breeder's knowledge on the relationship between kernel size and weevil resistance could be useful in determination of appropriate breeding strategies to be used in developing best cultivars.

Sorghum improvement: There is a need of developing biotic stress resistant sorghum cultivars to sustain sorghum productivity (Mofokeng *et al.*, 2016). Also, various studies highlighted traits that can be incorporated to improve sorghum resistance against storage insects including biophysical and biochemical traits which can improve both structural and or antibiosis mode of action (Bergvinson and Garcia-Lara, 2004). Most of the research targeting plant resistance through breeding concentrated on the integration of antibiotic and or antixenosis (Koch *et al.*, 2016). Sorghums have a wide variation of the type and level of biochemical molecules including protein resistant molecules, phenol composition and its content across the genotypes; these are determined by the genetics and environment (Awika and Rooney, 2004). According to Dykes and Rooney (2007) this valuable information assist breeders to develop sorghum varieties high in phenolics or desired compounds such as condensed tannins and special anthocyanins. Much that increased levels of these compounds on the sorghum kernel are important for weevil resistance, their optimum levels and or impact on sorghum yield needs to be established through scientific research.

Sources of resistance in sorghum to grain weevils: Several techniques have been employed to discriminate sorghum genotypes based on relative resistance; and the resistant genotypes can be selected as parental materials for weevil resistance in sorghum breeding programs (Young, 1977; Leuschner, 1994; Larrain *et al.*, 1995). Several resistance parameters such as kernel hardness, weight, oviposition, adult emergence, grain weight loss and median development period can be used to categorize genotypes based on their resistance (Adetunji, 1988; Prasad *et al.*, 2015). It is important to identify source of resistance from commercial varieties and advanced lines (Reddy *et al.*, 2006; Reddy *et al.*, 2008). When there is no resistant genotype, then screening of more genetically diverse sorghum germplasm such as gene bank accessions or wide-crosses can be done to look for alleles that are not present in cultivated sorghum cultivars (Reddy *et al.*, 2004); and when good sources for resistance are found biochemical basis must be evaluated to meet consumer needs, acceptability and safety so as to avoid some interference such as allergenic caused by

some protein based resistance and toxic biochemical's (Bergvinson and Garcia-Lara, 2004).

Currently, source of resistance for *Sitophilus spp.* among diverse sorghum genotypes has been identified in many places. For example, Reddy *et al.* (2002) found greater levels of antixenosis in terms of oviposition in genotypes “2077B, DJ 6514 and IS 11758” in a free-choice tests; and genotypes “2219B, M 148-138, P 721 and Nizamabad (M)” in a no-choice tests; and suggested the need to increase level of resistance in parental lines including A/B lines to be used hybrid making so as to protect sorghum from *Sitophilus oryzae*. Bamaïyi *et al.* (2007) categorised five more sorghum genotypes viz., BES, ICSV111, ICSV247, ICSV1079BF and ICSH89009NG as highly resistant genotypes *Sitophilus oryzae* due to lower F1 progeny emergence. Besides, Pradeep (2013) reported KMJ 1, CSV 216R, M 35-1, RSJ 1, and AKJ 1, as resistant sorghum varieties to *S. Oryzae* using percentage grain damage. Gofitshu and Belete, (2014) categorised sorghum genotype WB-77 as resistant variety to maize weevil; also, Prasad *et al.* (2015) categorised sorghum breeding lines “EC 22, EC 24, PEC 7, PEC 8, EP 57, EP 78 and AKR 354” as resistant genotypes to *Sitophilus spp.* and suggested the same to be employed in sorghum improvement programs for weevils resistance. In addition, Gerema *et al.* (2017) categorised “Lalo and Chemedra” as resistant sorghum varieties to *Sitophilus oryzae*. Therefore, it is important to transfer the insect resistance genes in sorghum into male-sterile (CMS), maintainer lines, and restorer lines to allow materials to be used by institutions in seed industry to develop grain weevil-resistant hybrids (Sharma *et al.*, 2005).

Breeding options in an effort of developing weevil resistant cultivars

Conventional breeding: Population improvement and selection through conventional breeding can be achieved for traits like resistance to *Sitophilus spp.* using conventional methodologies (Pérez-de-Castro *et al.*, 2012). Thus, breeders have to investigate genetic variability for grain weevil resistance and incorporate the traits in breeding line; through formation of segregating population which is followed by selection; where the selections are allowed to self-pollinate to produce pure-line cultivars; or test crossed to evaluate their worth as a parental line during hybrid making (Huang *et al.*, 2013). However, combination of conventional, modern breeding and genomics can be more useful, in characterizing weevil resistance in a diverse gene pool and incorporating resistance traits into useful sorghum cultivars (Dennis *et al.*, 2008).

Molecular breeding: The use of molecular breeding has been reported to be effective and can facilitate fast movement of one or two alleles even the recessive ones

(Collard and Mackill, 2008), despite the challenge of limited resources of genome sequencing especially in developing countries (Helmy *et al.*, 2016), genomic breeding are useful when dealing with complex traits, and can be used to develop more efficient sorghum cultivars using new methodologies such as genomic selection, marker assisted selection (breeding by design), association mapping and gene pyramiding (Pérez-de-Castro *et al.*, 2012) and can facilitate the identification of recessive allele and detection of QTLs. Various literature revealed the potential of the whole-genome sequencing in sorghum, in provision of intact genetic potential for improving landraces and preferred sorghum cultivars (Mace *et al.*, 2013). For instance, in marker assisted selection (MAS), selection is conceded out on the basis of a marker instead of the trait, due to the tight association between the marker and QTL or major gene associated with the trait; this facilitates the determination of desired traits even at early stages of breeding cycle. The genomic region in sorghum associated with resistance to *S. oryzae* has been identified; including 21 QTLs for grain weight loss (GLW), percentage kernel damage (PKD) and the flour production (FP) were mapped in chromosome 2 and can be used to understand weevils resistance mechanisms and be used to improve or develop resistant cultivars through marker assisted approaches (Zhai *et al.*, 2016).

Metabolomics assisted breeding is currently regarded as useful emerging strategy that can be used in genomics assisted breeding, with great potential in phenotyping and diagnostic analysis in sorghum, and should be taken as an addition tool in genomics assisted selection for crop improvement (Ferne and Schauer, 2009). Studies revealed the potential of metabolomics in characterizing biochemical variation within species, metabolic engineering and assessment of plant responses to the environment including biotic and abiotic stresses; furthermore, the genome Wide Association Mapping (GWAS) can be used to clearly connect the chemical variations of metabolomic profiles and their locations within the genome so as to assist in examining quantitative traits; and can be used as biomarkers in the prediction of traits (Turner *et al.*, 2016). This tool therefore, enables evaluation of the level of broad range of metabolites; and entails the effect of genetic diversity

on phenotypic variability in sorghum; In this case, metabolites related with heterosis could assist sorghum breeders in developing heterotic hybrids using molecular tools, though MAS of parental parents and improvement of parental lines for heterotic potential by marker assisted introgression of favourable allele; the use of Metabolome and protein profiling is critical in heterosis prediction because they signify likely targets for assessing heterosis appearance (Rajendrakumar, 2015).

Genetic engineering: According to Sharma *et al.* (2005), through genetic engineering, the metabolic pathways in sorghum may be altered to increase the level of secondary metabolites such as flavonoids; this might improve crop resistance to insect pest. Genetic transformation has been successful in cereal crops such as maize, wheat, barley and rice but has been difficult in sorghum (Moya, 2016). However, Sharma *et al.* (2005) revealed the possibility of developing insect resistant transgenic sorghums through incorporation of novel genes from *Bacillus thuringiensis*, plant lectins and or protease inhibitors; incorporation of these insecticidal genes will substitute the need for synthetic insecticides or any other grain weevil control strategies in sorghum and, therefore, eliminate or reduce environmental contamination resulted from use of synthetic chemicals; and the associated insect resistance. The use of genetic engineering in combination with natural sorghum resistance could assist genetic improvement of the crop in terms of yield and reduce susceptibility to insect pests including *Sitophilus* spp.

Description of weevil-sorghum interaction and its role in breeding: Sorghum interaction and its chemistry that can be used in developing resistant sorghum cultivars to *Sitophilus* spp. is as summarised in Fig 3. Various mechanisms can be drawn in the interaction including; weevil attack strategies, sorghum grain defensive strategies including antixenosis and antibiosis effects; and the related chemical compounds contributing to grain defence such as amylose, lysine content in protein, flavonoids, phenolic acids and condensed tannins. These traits can be exploited as source of resistance to weevils.

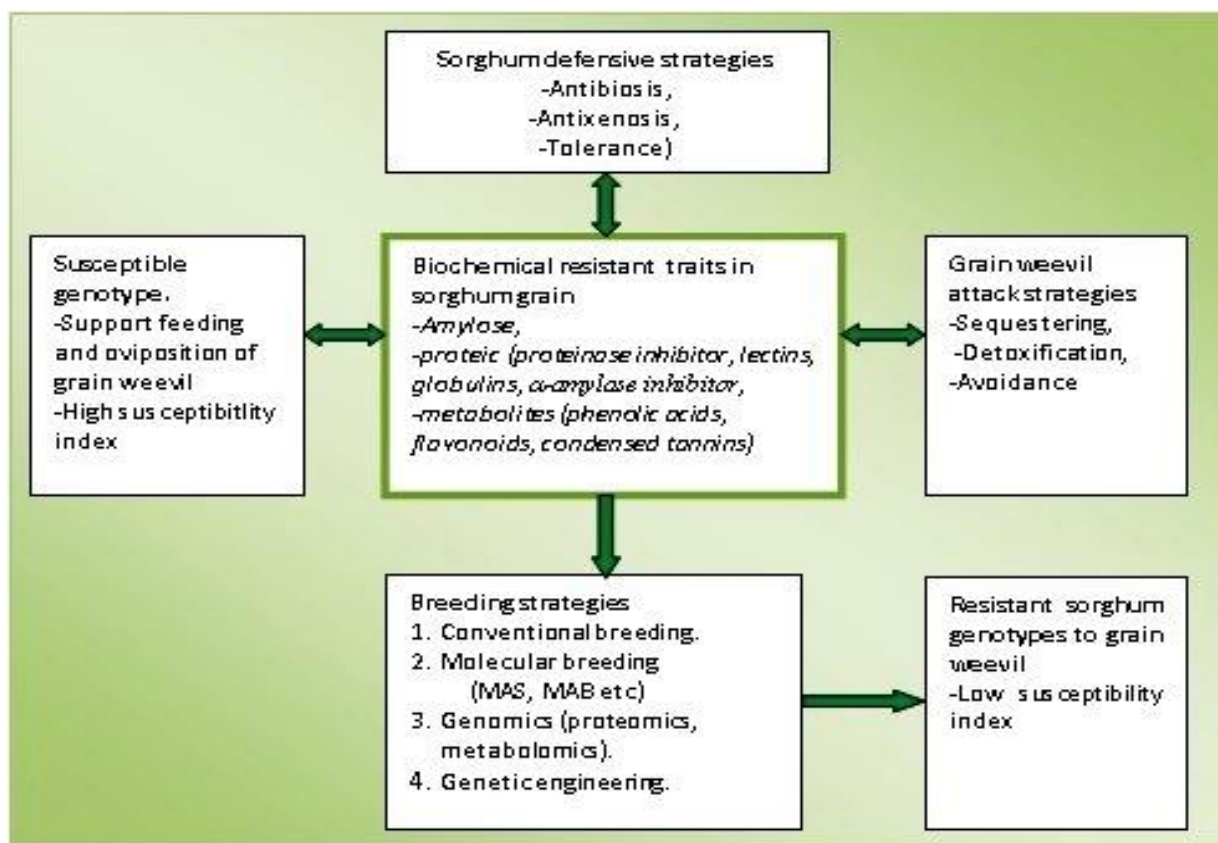


Figure 3. Model describing grain weevil-sorghum interaction and its role in breeding.

Conclusion: The interaction between sorghum and weevils (*Sitophilus* spp.) provides useful information on insect invasion strategies and host defensive mechanisms including chemical molecules. Apart from antibiosis and antixenosis effect to insect pest, these chemical molecules contribute in modulating grain hardness and strength, which are regarded as important phenotypic traits for grain resistance to weevil. Availability of these chemical defensive molecules in sorghum grain describes the level of grain susceptibility to weevils, where genotype with higher concentration of resistant protein and secondary metabolites can resist attacks and vice versa. It is worthwhile to note that, sorghum chemical related defensive traits are genetically based, and provide potential source of resistance, and can be exploited through various breeding options to develop new sorghum varieties with enhanced chemical related defence.

Acknowledgements: The authors acknowledge the Nelson Mandela African Institution of Science and Technology (NM AIST) especially the department of Sustainable Agriculture and Biodiversity Ecosystem Management; and department of sorghum and millets research from Tanzania Agricultural Research Institute (TARI – Ilonga) for their supports.

REFERENCES

- Abraha, T., S.M. Githiri, R. Kasili, W. Araia, and A. B. Nyende (2015). Genetic Variation among Sorghum (*Sorghum bicolor* L. Moench) Landraces from Eritrea under Post-Flowering Drought Stress Conditions. *Am J Plant Sci.* 6 (9):1410–1424.
- Adetunji, J. F. (1988). A study of the resistance of some sorghum seed cultivars to *Sitophilus Oryzae* (L.) (Coleoptera: Curculionidae). *J. Stored Prod. Res.* 24:67–71.
- Ajiboye, T. O., G.A. Iliasu, A.O. Adeleye, F. A. Abdussalam, S.A. Akinpelu, S.M. Ogunbode and, and O.B. Oloyede (2014). Nutritional and antioxidant dispositions of sorghum / millet-based beverages indigenous to Nigeria. *Food Sci Nutr.* 2(5):597–604.
- Awika, J. M. and L.W. Rooney (2004). Sorghum phytochemicals and their potential impact on human health. *Phytochemistry.* 65(9):1199–1221.
- Badigannavar, A., G. Girish, V. Ramachandran, and T.R. Ganapathi (2016). Genotypic variation for seed protein and mineral content among post-rainy season-grown sorghum genotypes. *Crop J.*

- 4(1):61–67.
- Balko, L. G. (1975). yield and quality of sorghum genotypes as affected by nitrogen and water. Univ. Texas.
- Bamaiyi, L.J., M.C. Dike, and I. Onu (2007). Relative Susceptibility of Some Sorghum Varieties to the Rice Weevil, *Sitophilus oryzae* L. (Coleoptera: Curculionidae). *J Entomol.* 4(5): 387–392
- Bennett, R. (1994). Secondary metabolites in plant defence. *New Phytol.* 127:617–633.
- Bergvinson, D. and S. Garcia-Lara (2004). Genetic approaches to reducing losses of stored grain to insects and diseases. *Curr Opin Plant Biol.* 7(4):480–485.
- Boisen, S. (1983). Protease Inhibitors in Cereals: Occurrence, Properties, Physiological Role, and Nutritional Influence. *Acta Agric Scand B.* 33(4):369–381.
- Boots, M., A. Best, M.R. Miller, and A. White (2009). The role of ecological feedbacks in the evolution of host defence: what does theory tell us?. *Philos Trans Royal Soc Lond B Biol Sci.* 364:27–36.
- Bustos-Segura, C., J. Formoni, and J. Nunez - Farfan (2014). Evolutionary changes in plant tolerance against herbivory through a resurrection experiment. *J. Evol. Biol.* 27(3):488–496.
- Chandrashekar, A. and K.V. Satyanarayana (2006). Disease and pest resistance in grains of sorghum and millets. *J. Cereal Sci.* 44(3): 287–304.
- Chandrashekar, A. and H. Mazhar (1999). The Biochemical Basis and Implications of Grain Strength in Sorghum and Maize. *J. Cereal Sci.* 30:193–207.
- Chippendale, G. M. (1972). Dietary Carbohydrates : Role in survival of the adult rice weevil, *Sitophilus Oryzae*. *J. Insect Physiol.* 18(5):949–957.
- Chiremba, C., J. R. N. Taylor, L.W. Rooney, and T. Beta (2012). Phenolic acid content of sorghum and maize cultivars varying in hardness. *Food Chem.* 134(1):81–88.
- Cheng, S., Y. Sun, and L. Halgreen (2009). The Relationships of Sorghum Kernel Pericarp and Testa Characteristics with Tannin Content. *Asian J. Crop Sci.* 1(1): 1–5.
- Clark, R.B, C. I. Flores, L. M. Gourley, and R. R. Duncan (1990). Mineral element concentrations and grain yield of sorghum (*Sorghum bicolor*) and pearl millet (*Pennisetum glaucum*) grown on acid soil. In M.L. Van Beusichem (eds) *Plant Nutrition — Physiology and Applications. Developments in Plant and Soil Science.* Springer. pp. 391–396.
- Collard, B. C. Y. and D.J. Mackill (2008). Marker-assisted selection : an approach for precision plant breeding in the twenty-first century. *Philos Trans R Soc Lond B Biol Sci.* 363:557–572.
- CTA. (1998). Larger grain borer *Prostephanus truncatus*: Technical leaflet No. 1.
- Dal Bello, G., S. Padin, C. López Lastra, and M. Fabrizio (2000). Laboratory evaluation of chemical-biological control of the rice weevil (*Sitophilus oryzae* L.) in stored grains. *J. Stored Prod. Res.* 37(1):77–84.
- Dasbak, M. A., B.C.Echezona, and J.E. Asiegbe (2009). Pigeon pea grain physical characteristics and resistance to attack by the bruchid storage pest. *Agrophysics.* 23(1): 19–26.
- Dennis, E. S., J. Ellis, A. Green, D. Llewellyn, M. Morell, L. Tabe, and W.J. Peacock (2008). Genetic contributions to agricultural sustainability. *Philos Trans R Soc Lond B Biol Sci.* 363:591–609.
- Dent, D. (2000). *Insect Pest Management 2nd Edition*; CABI Bioscience.
- Dicko, M. H. (2005). Endogenous phenolics and starch modifying enzymes as determinants of sorghum for food use in Burkina Faso. Univ. Wageningen.
- Dobie, P. (1977). Contribution of the tropical stord product centre to the study of insect resistance in stored maize. *Tropical Stored Product Information.* 34:7–2.
- Dykes, L. and L. W. Rooney (2006). Sorghum and millet phenols and antioxidants. *J Cereal Sci.* 44:236–251.
- Dykes, L. and L. W. Rooney (2007). Phenolic compounds in cereal grains and their health benefits. *Cereal Food World.* 52(3):105–111.
- Dykes, L., L.W. Rooney, R.D. Waniska, and W.L. Rooney (2005). Phenolic compounds and antioxidant activity of sorghum grains of varying genotypes. *J. Agrc. Food Chem.* 53(17):6813–6818.
- Dykes, L., L.H. Jr, O. Portillo-Rodriguez, W.L. Rooney, and L.W. Rooney (2014). Prediction of total phenols, condensed tannins, and 3-deoxyanthocyanidins in sorghum grain using near-infrared (NIR) spectroscopy. *J. Cereal Sci.* pp 1-5
- Dykes, L., L. M. Seitz, W. L. Rooney, and L.W. Rooney (2009). Flavonoid composition of red sorghum genotypes. *Food Chem.* 116:313–317.
- Earp, C. F. and L.W. Rooney (1982). Scanning Electron Microscopy of the Pericarp and Testa of Several Sorghum Varieties. *Food Microstructure.* 1(3): 125–134.
- Earp, C.F., C.M. McDonough, and L.W. Rooney (2004). Microscopy of pericarp development in the caryopsis of *Sorghum bicolor* (L.) Moench. *J Cereal Sci.* 39(1): 21–27.

- Ebadi, M. R., J. Pourreza, J. Jamalain, M.A.Edriss, A.H. Samie, and S.A. Mirhadi (2005). Amino Acid Content and Availability in Low , Medium and High Tannin Sorghum Grain for Poultry. *Int J Poult Sci.* 4(1):27–31.
- Felix, K., E. Cheruiyot, C.M. Mwenda, C.K. Erick, and N.F. Wachira (2015). Nutritional suitability of bred sorghum (*Sorghum bicolor*) accessions from East Africa. *Afr. J. Food Sci.* 9(5):326–333.
- Fernie, A. R. and N. Schauer (2009). Metabolomics-assisted breeding: a viable option for crop improvement. *Trends Genet.* 25(1):39–48.
- Fürstenberg-hägg, J., M. Zagrobelny, and S. Bak (2013). Plant Defense against Insect Herbivores. *Int J Mol Sci.* 14:10242–10297.
- Geleta, N. and M.T. Labuschagne (2005). Qualitative traits variation in sorghum (*Sorghum bicolor* (L.) Moench) germplasm from eastern highlands of Ethiopia. *Biodiversity and Conservation.* 14: 3055–3064.
- Gerema, G., T. Bogale, G. Mangistu, and D. Lule (2017). Resistance of sorghum genotypes to the rice weevil, *Sitophilus oryzae* (L.) (coleoptera curculionidae). *Int J Food Sci Technol.* 7(1):1–10.
- Gerrano, A. S., M. T. Labuschagne, A. V. Biljon, and N.G. Shargie (2014). Genetic variability among sorghum accessions for seed starch and stalk total sugar content. *Sci. Agric.* 71(6):472–479.
- Goftishu, M. and K. Belete (2014). Susceptibility of sorghum varieties to the maize weevil *Sitophilus zeamais* Motschulsky (Coleoptera : Curculionidae). *Afr. J. Agric. Res.* 9(31):2419–2426.
- Gracen, V. E. and W.D. Guthrie (2008). Host plant resistance for insect control in some important crop plants. *Crit Rev Plant Sci.* 4(3):277–291.
- Gu, H., O. R. Edwards, A. T. Hardy, and G. P. Fitt (2008). Host plant resistance in grain crops and prospects for invertebrate pest management in Australia: an overview. *Aust J Exp Agric. Csiro Publishing.* 48(12):1543–1548.
- Hagerman, A. (2002). Condensed Tannin Structural Chemistry. *Tannin Chemistry.* Univ. Miami.
- Helmy, M., M. Awad, and K. A. Mosa (2016). Limited resources of genome sequencing in developing countries: Challenges and solutions. *Appl Transl Genom.* 9:15-19.
- Hernandez, C. E. C. (2012). Effects of Sorghum Digestibility, Endosperm Texture and Type Phenolic Profile on Postharvest Resistance to Maize Weevil and Fuel Ethanol Production. *Univ. Tecnológico De Monterrey.*
- Holding, D. R. (2014). Recent advances in the study of prolamins storage protein organization and function. *Front Plant Sci.* 5:(276)1–10.
- Huang, Y., H.C. Sharma, and M.K. Dhillon (2013). Bridging Conventional and Molecular Genetics of Sorghum Insect Resistance. In A. Paterson (eds) *Genomics of the Saccharinae. Plant Genetics and Genomics: Crops and Models.* Springer. New York. 11:367–389.
- Hulse, J.H., E.M. Laing, and O. E. Pearson (1980). Sorghum and the millets: Their composition and nutritive value. *Academic Press, London.*
- Jadhav, K. (2006). Biology and management of rice weevil, *Sitophilus oryzae* L. in pop sorghum. *Univ. Agric Sci. Dharwad.*
- Kant, M. R., W. Jonckheere, B. Knecht, F. Lemos, J. Liu, B.C.J. Schimmel, C.A. Villarroel, L. M. S. Ataide, W. Dermauw, J. J. Glas, M. Egas, A. Janssen, T. Van Leeuwen, R. C. Schuurink, M. W. Sabelis, and J. M. Alba (2015). Mechanisms and ecological consequences of plant defence induction and suppression in herbivore communities. *Ann. Bot.* 115(7):1015–1051.
- Keskin, S. and H. Ozkaya (2013). Effect of storage and insect infestation on the mineral and vitamin contents of wheat grain and flour. *J Econ Entomol.* 106(2):1058–1063.
- Khalil, J. K., W.N. Sawaya, W. J. Safi, and H. M. Al-Mohammadm (1984). Chemical composition and nutritional quality of sorghum flour and bread. *Plant Foods for Hum Nutr.* 34:141–150.
- Koch, K.G., K. Chapman, J. Louis, T. Heng-Moss, and G. Sarath (2016). Plant Tolerance: A Unique Approach to Control Hemipteran Pests. *Front Plant Sci.* 7:1363.
- Kulamarva, A. G., V.R. Sosle, and G.S.V. Raghavan (2012). Nutritional and Rheological Properties of Sorghum. *Int J Food Prop.* 12:55–69.
- Kumar, T., I. Dweikat, S. Sato, Z. Ge, N. Nersesian, H. Chen and T. Elthon, S. Bean, B.P. Loerger, M. Tilley, and T. Clemente (2012). Modulation of kernel storage proteins in grain sorghum (*Sorghum bicolor* (L.) Moench). *Plant Biotechnol J.* 10:533–544.
- Ladang, Y. D., L. S. T. Ngamo, M.B. Ngassoum, P. M. Mapongmestsem, and T. Hance (2008). Effect of sorghum cultivars on population growth and grain damages by the rice weevil , *Sitophilus oryzae* L . (Coleoptera : Curculionidae). *Afr. J. Agric. Res.* 3(2):255–258.
- Larrain, P. I., J.E. Araya, and J.D. Paschke (1995). Methods of infestation of sorghum lines for the evaluation of resistance to the maize weevil, *Sitophilus zeamais* Motschulsky (Coleoptera : Curculionidae). *Crop Prot.* 14:561–564.
- Lattanzio, V., V.M.T. Lattanzio, and A. Cardinali (2006). Role of phenolics in the resistance mechanisms of plants against fungal pathogens and insects.

- Phytochemistry: Advances in Research. 37:23-67.
- Leuschner, K. (1994). Methodology for Screening Sorghum Resistance to Storage Pests. *Oar.icrisat.org*.
- Longstaff, B. C. (1981). Biology of the grain pest species of the genus *sitophilus* (coleoptera: curculionidae): A critical review. *Prot Ecol*. 2:83-130.
- Mabelebele, M., M. Siwela, R.M. Gous, and P.A. Iji (2015). Chemical composition and nutritive value of South African sorghum varieties as feed for broiler chickens. *S. Afr. J. Anim. Sci*. 45:206-213.
- Macauley, H.R. (2015). Cereal Crops: Rice, Maize, Millet, Sorghum, Wheat. *Background Paper*.
- Mace, E.S., S.Tai, E.K.Gilding, Y.Li, P.J.Prentis, L.Bian, B.C.Campbell, W.Hu, D.J.Innes, X.Han, A.Cruickshank, C.Dai, C.Frère, H.Zhang, C.H.Hunt, X.Wang, T.Shatte, M.Wang, Z.Su, J.Li, X.Lin, I.D.Godwin, D.R.Jordan, and J.Wang (2013). Whole-genome sequencing reveals untapped genetic potential in Africa's indigenous cereal crop sorghum. *Nat Commun*. Macmillan Publishers Limited.
- Mafuru, J.M., D.W. Norman, and Fox J.S (2016). Consumer Perception of Sorghum Variety Attributes in the Lake Zone Tanzania. In *AAAE Conference Proceedings* (pp. 171-176).
- Mason, L. J. and M. McDonough (2012). Biology, Behavior, and ecology of stored grain and legume insects. In *stored product protection*. Kansas State University Agricultural Experiment Station and Cooperative Extension Service. pp.1-14.
- Mello, M. O. and M.C. Silva-filho (2002). Plant-insect interactions: An evolutionary arms race between two distinct defense mechanisms. *Braz. J. Plant Physiol*. 14(2):71-81.
- Mendesil, E., C. Abdeta, A. Tesfaye, Z. Shumeta, H. Jifar (2007). Farmers perceptions and management practices of insect pests on stored sorghum in southwestern Ethiopia. *Crop Prot*. 26:1817-1825.
- Mendesil, E. (2014). Plant-resistance to insect herbivores and semiochemicals: plant-resistance to insect herbivores and semiochemicals. Swedish Univ. Agric Sci. Published by SLU.
- Mofokeng, M. A. (2016). Control strategies and breeding efforts in sorghum for resistance to storage weevils Control strategies and breeding efforts in sorghum for resistance to storage weevils. *Afr. J. Agric. Res*. 11(33):3065-3073.
- Mofokeng, M. A., H. Shimelis, P. Tongoona, and M.D. Laing (2016). Constraints and varietal trait preferences of sorghum producers in South Africa. *Trop Agric*. 54:7-15.
- Mofokeng, A. M., H.Shimelis, and M. Laing (2017). Breeding strategies to improve sorghum quality of South Africa. *Aust J Crop Sci*. 11(2):142-148.
- Mosse, J., J.C. Huet, and J. Baudet (1988). The amino acid composition of whole sorghum grain in relation to its nitrogen content. *Cereal Chem*. 65(4):271-277.
- Moya, M. (2016). Lysine genetically enriched cereals for improving nutrition in children under 5 years in low- and middle- income countries. *J Nutr Health Food Eng*. 5:1-5.
- Mukarumbwa, P. and A. Mushunje (2010). Potential of sorghum and finger millet to enhance household food security in Zimbabwe 's semi-arid regions: A review. African Association of Agricultural Economists and Agricultural Economists Association of South Africa Conference. Cape Town, South Africa.
- Murthy, K. S. and M. A. Ahmed (1978). Effect of some characters of different sorghum varieties on the development of rice weevil, *Sitophilus oryzae*. *Bulletin of Grain Tech*. 16: 48-50.
- Mutisya, J. (2004). *Starch Branching Enzymes and their Genes in Sorghum*. Univ. Agric Sci, Uppsala.
- Muzemu, S., J. Chitamba, and S. Goto (2013). Screening of Stored Maize (*Zea mays* L.) Varieties Grain for Tolerance Against Maize Weevil , *Sitophilus zeamais* (Motsch.). *Int. J. Plant. Res*. 3(3):17-22.
- Nwosu, L. C., C.O. Adedire, and E.O. Ogunwolu (2015). Screening for new sources of resistance to *Sitophilus zeamais* Motschulsky (Coleoptera : Curculionidae) infestation in stored maize genotypes. *J. Crop Prot*. 4(3):277-290.
- Ogolla, A E., N. Njau, P. Mwirigi, C. W. Muui, N. K. Kibet, and M. Mwangi (2016). Climate change effects on rainfall patterns and its implications on sorghum and millet production in Kenya : A Review. *Int. J. Sci. Technol*. 4:44-52.
- Oyier, M., J. Owuoch, E. Cheruiyot, M. Oyoo, and J. Rono (2016). Utilization of Sorghum (*Sorghum bicolor* L . Moench .) hybrids in Kenya : A review. *Int. J. Agron. Agric. Res*. 9(6):65-75.
- Painter, R. H. (1951). Insect resistance in crop plants. *Macmillan, New York*.
- Pendleton, M.W., B.B. Pendleton, E. A. Ellis, G.C. Peterson, F. M. Chitio, and S. Vyavhare (2011). Correlation of resistance to maize weevil, *Sitophilus zeamais*, and starch arrangement in sectioned kernels of sorghum. *Microsc Microanal*. 17:2.
- Pfeiffer, B.K., and W. Rooney (2015). Inheritance of Pericarp Color, Nutritional Quality, and Grain Composition Traits in Black Sorghum. *Crop*

- Breed Genet. 56:164–172.
- Pontieri, P., J. Troisi, R. Di-Fiore, A.D. Maro, S.R. Bean, M.R. Tuinstra, E. Roemer, A. Boffa, A.D. Giudice, G. Pizzolante, P. Alifano and L.D. Giudice (2014). Mineral contents in grains of seven food-grade sorghum hybrids grown in a Mediterranean environment. *Aust J Crop Sci.* 8:1550–1559.
- Pradeep. (2013). Screening of Rabi Sorghum genotypes for resistance against rice weevil [*Sitophilus oryzae* (L.)] and management through Botanicals. Univ. Agric Sci, Dharwad.
- Prajapati, D. R., Pahuja, S. K., Verma, N. K., and S. Chaudhary (2018). Morphological Characterization of Sorghum [*Sorghum bicolor* (L.) Moench] Germplasm for DUS Traits. *Int J Curr Microbiol Appl Sci.* 7(2):2058–2071.
- Prasad, G.S., K. S. Babu, M. Sreedhar, P.G. Padmaja, B. Subbarayudu, A. Kalaisekar, and J.V. Patil (2015). Resistance in sorghum to *Sitophilus oryzae* (L.) and its association with grain parameters. *Phytoparasitica.* 43(3):391–399.
- Rajendrakumar, P. (2015). Heterosis Prediction Using DNA Markers. In: R. Madhusudhana, P. Rajendrakumar, J. Patil (eds) *Sorghum Molecular Breeding*. Springer, New Delhi. Springer. pp. 102–110.
- Ramputh, A., A. Teshome, D.J. Bergvinson, C. Nozzolillo, and J.T. Arnason (1999). Soluble phenolic content as an indicator of sorghum grain resistance to *Sitophilus oryzae* (Coleoptera: Curculionidae). *J Stored Prod Res.* 35(1):57–64.
- Ratnavathi, C.V. and J.V. Patil (2013). Nutrition & Food Sorghum Utilization as Food. *J Nutr Food Sci.* 4(1):1–8.
- Reddy, B.V.S., A.A. Kumar, and P.S. Reddy (2008). Genetic improvement of sorghum in the semi-arid tropics. In B.V.S. Reddy (Ed.), *Sorghum Improvement in the New Millennium*. ICRISAT, Patancheru, Andhra Pradesh, India. pp. 105–123.
- Reddy, B.V.S., P. Rao, U.K. Deb, J.W. Stenhouse, B. Ramaiah, and R. Ortiz (2004). Global sorghum genetic enhancement processes at ICRISAT. In: M.C.S. Bantilan, U.K. Deb, C.L.L. Gowda, B.V.S. Reddy, A.B. Obilana and R.E. Evenson (eds.) 2004. *Sorghum genetic enhancement: research process, dissemination and impacts*. ICRISAT, Patancheru, Andhra Pradesh, India. pp. 65–101.
- Reddy, B.V.S., H.C. Sharma, R.P. Thakur, S. Ramesh, F. Rattunde, and M. Mgonja (2006). Sorghum hybrid parents research at ICRISAT – strategies, status, and impacts seed parents' research at ICRISAT-Patancheru, India. *SAT eJournal* | Ejournal.icrisat.org. 2:1–24.
- Reddy, K. P. K., B.U. Singh, and K.D. Reddy (2002). Sorghum resistance to the rice weevil, *Sitophilus oryzae* (L.): Antixenosis. *Insect Sci. Applic.* 22(1):9–19.
- Rooney, L. W. and F.R. Miller (1981). Variation in the Structure and Kernel Characteristics of sorghum. In: L. W. Rooney D. S. Murty and J. V. Martin (eds.), *International Symposium on Sorghum Grain Quality*. ICRISAT, Patancheru, India. pp. 143–162.
- Russell, M. (1962). Effects of Sorghum Varieties on the Lesser Rice Weevil, *Sitophilus oryzae* (L.), Oviposition, Immature Mortality, and Size of Adults. *Ann Entomol Soc Am.* 55(6): 678–685.
- Russell, P. (1966). Effects of four sorghum varieties on the longevity of the lesser rice weevil, *Sitophilus oryzae* (L.). *J Stored Prod Res.* 2(1):75–79.
- Salem, E. M. M. (2015). Response of grain sorghum (*Sorghum bicor* L. Monech) to irrigation, nitrogen and plant density under new valley conditions Egypt. *Egyptian J. Desert Res.* 65:11–30.
- Salunkhe, D. K., S. S. Kadam, and J. K. Chavan (1977). Nutritional quality of proteins in grain sorghum. *Qual. Plant. Plant Food Hum Nutr.* 27:187–205.
- Sang, Y., S. Bean, P.A. Seib, J. Pedersen, and Y.C. Shi. (2008). Structure and functional properties of sorghum starches differing in Amylose Content. *J. Agric. Food Chem.* 56(15):6680–6685.
- Sastry, L. V. S., J.W. Paulis J.A. Bietz, and J.S. Wall (1986). Genetic variation of storage proteins in sorghum grain: Studies by Isoelectric Focusing and High-Performance Liquid Chromatography. *Cereal Chem.* 63(5):420–427.
- Saxena, M., J. Saxena, R. Nema, D. Singh, and A. Gupta. (2013). *Phytochemistry of Medicinal Plants*. J Pharmacogn Phytochem. 1(6):168–182.
- Sedghi, M., A. Golian, P. Soleimani-Roodi, A. Ahmadi, and M. Aami-Azghadi (2012). Relationship between color and tannin content in sorghum grain: application of image analysis and artificial neural network. *Braz J Poultry Sci.* 14(1):57–62.
- Sharma, H. C. (1993). Host-plant resistance to insects in sorghum and its role in integrated pest management. *Crop Prot.* 12: 11–34.
- Sharma, H.C., B.V.S. Reddy, M.K. Dhillon, K. Venkateswaran, B.U. Singh, G. Pampapathy, R.T. Folkertsma, C.T. Hash, and K.K. Sharma (2005). Host Plant Resistance to Insects in Sorghum: Present Status and Need for Future Research. *International Sorghum and Millets Newsletter.* 46:36–43.
- Sinha, S. and N. Kumaravadivel (2016). Understanding Genetic Diversity of Sorghum Using

- Quantitative Traits. Hindawi. Scientifica.2016:1-8.
- Smith, C.M. (2005). *Plant Resistance to Arthropods*. Chapt 2: Antixenosis - Adverse Effects of Resistance on Arthropod Behavior. Plant Resistance to Arthropods. Springer, Dordrecht, Netherland pp.19-63.
- Stejskal, V. and Z. Kučerová (1996). The effect of grain size on the biology of *Sitophilus granarius* L. (Col., Curculionidae). Oviposition, distribution of eggs and adult emergence. J Appl Entomol.120(1): 143–146.
- Talebi, K., V. Hosseiniaveh, and M. Ghadamyari (2011). Ecological impacts of pesticides in agricultural ecosystem. In: M. Stoytcheva (eds), Pesticides in the Modern World - Risks and Benefit. pp. 143–168.
- Torres, J.B., J.L.D. Saavedra, J.C Zanuncio, and J. M.Waquil (1996). Resistance-sorghum to *Sitophilus oryzae* (L.) and its association with varietal parameters. Int J Pest Manag. 42(4):277–280.
- Turner, M. F., A. L.Heuberger, J.S. Kirkwood, C.C. Collins, E.J. Wolfrum, C.D. Broeckling, J.E. Prenni, and C.E. Jahn (2016). Non-targeted metabolomics in diverse sorghum breeding lines indicates primary and secondary metabolite profiles are associated with plant biomass accumulation and photosynthesis. Front Plant Sci. 7: 953.
- Venkatrao, S., R. N. Nuggewailli, M. Swaminathan, S. V. Pingare, and V.Subrahmanyam (1958). Effect of insect infestation on stored grain. J. Sci. Food Agric. 3(837):1957–1959.
- Pérez-de-Castro, A.M., S. Vilanova, J. Cañizares, L. Pascual, J.M. Blanca, M.J. Díez, J. Prohens, and B. Picó (2012). Application of genomic tools in plant breeding. Curr Genom. 13:179–195.
- USDA. (2013). Grain Inspection Handbook. Book II , Sorghum.
- Vieira, A., C.Santana, C.Bezerra, D. Menezes, and R. Eugene (2015). Nutritional composition of sorghum [sorghum bicolor (L .) Moench] genotypes cultivated without and with water stress. J Cereal Sci. 65: 103–111.
- Virupaksha, T.K. and L.V.S. Sastry (1968). Studies on the protein content and amino acid composition of some varieties of grain sorghum. J. Agric. Food Chem. 16:199–203.
- Wall, J. S. and C.W. Blessin (1969). Composition ~ Structure of Sorghum Grains. Cereal Sci Today. 14:264-271.
- Waniska, R. D. (2000). Structure, Phenolic Compounds, and Antifungal proteins of sorghum caryopses. In: A. Chandrashekar, R. Bandyopadhyay and A.J. Hall. (Eds), Technical and institutional options for sorghum grain mold management: Proceeding of an International consultation. ICRISAT, Patancheru, Andhra Pradesh, India. pp. 72–106.
- Waniska, R.D, L.W. Rooney, and C. McDonough (2004). Sorghum/utilization. In C.W.Wrigley, H. Corke, C.E. Walker. Encyclopedia of grain science. Elsevier. pp.126–38.
- War, A. R., M. G. Paulraj, T. Ahmad, A.A. Buhroo, B. Hussain, S.Ignacimuthu, and H.C. Sharma (2012). Mechanisms of Plant defense against insect herbivores. Plant Signal Behav. 7(10):1306–1320.
- Weledesemayat, G. T., T. B. Gezmu, A.Z. Woldegiorgis, and H.F.Gemede (2016). Study on Aspergillus Species and Aflatoxin Levels in Sorghum (*Sorghum bicolor* L.) Stored for Different Period and Storage System in Kewet Districts, Northern Shewa. J Food Sci Nutr. 2(10):1–8.
- Williams, J. O. (1978). Factors Related to Rice Weevil Resistance. Deptt. of Entom., Univ. Kansas.
- Wongo, L. E. (1990). Factors of resistance in sorghum against *Sitotroga cerealella* (Oliv.) and *Sitophilus oryzae* (L.). Int J Trop Insect Sci.11(2), 179–188.
- Wongo, L.E. (1998). Biological activity of sorghum tannin extracts on the stored grain pests *sitophilus oryzae* (L), *sitotroga cerealella* (olivier) and *Tribolium castaneum* (Herbst). Insect Sci. Appl. 18(1):17–23.
- Wu, Y., D.R.Holding, and J. Messing (2010). γ - Zeins are essential for endosperm modification in quality protein maize. Proc Natl Acad Sci USA. 107:12810–12815.
- Wu, Y., X.Li, W.Xiang, C. Zhu, Z. Lin, Y.Wu, and J. Li (2012). Presence of tannins in sorghum grains is conditioned by different natural alleles of Tannin1. Proc Natl Acad Sci USA. 109(26):10281–10286.
- Young, W. R. (1977). Sorghum entomology. Ann. Rev. Entom. 22:193–218.
- Zhai, G., H. Wang, S. Li, H. Liu, J. Shao, Y.Tao, and G. Zou (2016). Identification of genomic region associated with rice weevil resistance in sorghum [*Sorghum bicolor* (L.) Moench]. J Stored Prod Res. 69:166–171.